

IV. "Preliminary Account of the Nephridia and Body Cavity of the Larva of *Palæmonetes varians*." By EDGAR J. ALLEN, B.Sc., University College, London. Communicated by Professor W. F. R. WELDON, F.R.S. Received November 17, 1892.

The researches of which the present communication contains a brief summary, were carried on during the summer of the present year, at the Laboratory of the Marine Biological Association in Plymouth, where I occupied a table by appointment of the British Association Committee. The observations were made chiefly on larvæ of *Palæmonetes varians*, but other species have also been included, and will be mentioned in particular instances.

I. *The Nephridia.*

During the greater part of the larval life two pairs of nephridia are present: the green glands, which open at the bases of the second antennæ, and the shell glands, which open at the bases of the second maxillæ.

The Green Gland.—In a larva of *Palæmonetes* which is a few days old, the green gland has a form similar to that described by Weldon* and Marchal† for the adult of *Virbius*, *Pandalus*, and *Crangon*, excepting that the remarkable enlargements of the bladder, which the former author has termed "nephroperitoneal sacs," are not as yet developed. The gland consists of an end sac, which communicates by means of a U-shaped tube with a very short ureter opening at the base of the antenna. The distal portion of the tube is slightly enlarged, and may be called the bladder. At the time of hatching of the larva, the whole gland consists of a solid mass of cells, in which no cavity has appeared, although the portions which afterwards form the end sac and the tube can be distinguished, and the ureter and external opening are already present. Shortly after the larva has become free the cells separate, and give rise to the lumen of the gland.

The later development of the green gland consists chiefly in the enlargement of the bladder, which grows at first inwards, towards the middle ventral line of the body, then upwards, within the œsophageal nerve ring, and anterior to the œsophagus, to the middle

* Weldon, W. F. R., "The Renal Organs of certain Decapod Crustacea." 'Quart. Journ. Micr. Sci.,' vol. 32, 1891.

† Marchal, P., "Recherches anatomiques et physiologiques sur l'appareil excréteur des Crustacés Décapodes." 'Arch. Zool. Expér.,' vol. 10, 1892.

dorsal line, where it meets its fellow of the opposite side. The two bladders grow backwards over the stomach, subsequently fusing in the middle line to form the unpaired nephroperitoneal sac. This mode of development confirms the view as to the nature of the latter sac already arrived at by Weldon and Marchal from a comparative study of the renal organs of Decapods.

The Shell Gland.—In a figure of a *Callinassa* larva in the *Mysis* stage, Claus* inserts and names the shell gland, opening at the base of the second maxilla. This is, I believe, the only recorded instance of the gland having been recognised in a Decapod, unless, indeed, the "segmental organ" described by Lebedinski† as opening at the base of the first maxillipede of the larva of *Eriphya spinifrons*, and communicating with the body cavity, be the same organ.

In late embryos, and at the time of hatching of the larva, the shell glands are the functional kidneys of *Palæmonetes* and *Palæmon*, the green gland being still without a lumen. The shell gland of *Palæmonetes* consists of a comparatively short renal tube, with a considerable lumen, which communicates internally with an end sac, and opens externally at the base of the second maxilla. The general form of the tube may be expressed by saying that it is Y-shaped, the two arms of the Y being in a horizontal plane, with the end sac attached to the internal one, whilst the leg of the Y is curved in a vertical plane, the concavity looking downwards and backwards. The histological structure of both end sac and renal tube is similar to that described by Grobben‡ for the green gland of *Mysis*. The entrance from the end sac to the tube is guarded, however, by a valve, formed of elongated cells of the end sac, which does not appear to have been found in other forms.

I have detected no trace of the shell gland in young adults.

§II. *The Body Cavity.*

The Anterior Region of the Thorax.—A transverse section through the region of the second maxillæ of a *Palæmonetes* larva, which is a few days old, shows that the cavity enclosed by the external chitin and ectoderm may be divided into four regions: a *dorsal sac*, surrounded by a definite layer of epithelium, and within which the cephalic aorta lies, but which does not itself contain blood; a *central cavity*, in which the liver, intestine, and nerve cord, are found; two

* Claus, C., "Neue Beiträge zur Morphologie der Crustaceen." 'Arb. Zool. Inst. Wien,' vol. 6, 1886.

† Lebedinski, J., "Einige Untersuchungen über die Entwicklungsgeschichte der Seekrabben." 'Biol. Centralbl.,' vol. 10, 1890.

‡ Grobben, C., "Die Antennendrüse der Crustaceen." 'Arb. Zool. Inst. Wien,' vol. 3, 1881.

lateral cavities, separated from the central cavities by masses of muscle and bands of connective tissue, and which, in the region under consideration, contain the proximal ends of the shell glands; and, fourthly, the *cavities of the limbs*, which contain the distal ends of the same organs. The cavities of the limbs communicate with the lateral cavities, and the latter frequently communicate with the central cavity by the disappearance of the connective tissue bands. The central cavity, the lateral cavities, and the cavities of the limbs, all contain blood.

The Dorsal Sac.—I have found the dorsal sac in *Palæmon serratus*, *Palæmonetes varians*, and *Crangon vulgaris*, and in the adult it attains a considerable size. If a dissection be made of an adult *Palæmon*, the sac is readily seen. Anteriorly it appears as an elongated, cylindrical tube, lying upon the nephroperitoneal sac, and containing within it the cephalic aorta. Posteriorly it is very much enlarged, covering the front part of the ovaries, and running downwards on either side into the cavity which surrounds the intestine and liver. A similar condition of things is found in the adult *Palæmonetes*.

The dorsal sac does not contain blood. I have been led to this conclusion for the following reasons:—(1.) In a large number of series of sections, both of larvæ and adults, I have never seen a blood corpuscle within the sac. (2.) The sac is completely closed, and has no communication with the blood sinuses of the body. In preserved specimens it contains a clot, which can generally be distinguished from the surrounding blood clot. (3.) I have observed carefully, and for a long time, living larvæ, and the space occupied by the sac has always been perfectly free from blood corpuscles.

At its anterior end the dorsal sac is surrounded by a mass of tissue, from the external surface of which blood corpuscles appear to be budding off. Before commencing this research, Professor Weldon, to whom the existence of this tissue was known, and who has indicated it in his figures, suggested to me this view of its nature, and it is fully supported by my preparations.

Development of the Dorsal Sac.—In embryos of *Palæmonetes* in which the cephalic aorta is already formed, the cells surrounding the latter are arranged in two layers, an internal and an external. Before the time of hatching arrives, the cells of the external layer enlarge considerably, and give rise to the appearance of a solid mass of cells upon either side of the aorta. The dorsal sac is formed by the hollowing out of these masses of cells. Two lateral cavities are thus formed, which are separated by the aorta. The protoplasm of the cells lining these cavities, which is at first gathered into masses around the nuclei, then spreads out into a thin sheet, drawing away from the lower portion of the aorta, and causing the two lateral cavities to unite ventrally, and so form a single sac. In the region of the first

and second maxillæ, all the stages of the process just described may be seen. In the region anterior to this I have never actually observed the stage with two lateral cavities, the two having always united ventrally, but I do not doubt that the process is here the same as in the posterior region.

In one series of sections of a larva, preserved very soon after it had left the egg, the cavity was formed upon either side of and below the aorta, as far back as the anterior end of the segment of the first maxillæ, where for one section it was almost completely closed. Behind this the condition with two lateral cavities was found, and persisted through the region of the first maxillæ, whilst in the region of the second maxillæ no cavity had yet opened, and solid masses of cells still lay upon either side of the aorta.

The further development of the dorsal sac consists mainly of an increase in its size. At its posterior end it grows backwards in a pair of lobes, which extend as far as the front end of the pericardium.

The Posterior Region of the Thorax.—The central and lateral cavities are here similar to those of the anterior region, whilst dorsal to them the pericardial chamber lies. This chamber is separated from the central body cavity, as is already well known, by the pericardial septum, and it contains the heart. The genital organs are situated at the front end of the pericardium, immediately below the pericardial septum. In the just-hatched larva these consist of two masses of cells with large nuclei, each mass being enclosed in a sheath of mesoderm. I have not detected any trace of the genital ducts at this stage.

The Abdomen.—With regard to the abdomen, my sections confirm the accounts given by Milne Edwards* and Claus.† There are two main sinuses, which run along its length: a dorsal sinus, in which the intestine lies, and a ventral one, which contains the nerve cord. These two sinuses are generally separated by masses of muscle, but they communicate at intervals by means of lateral sinuses.

Theoretical Considerations.

The state of the body cavity in the anterior region of the thorax of *Palæmonetes* may be compared with that of *Peripatus*, as described by Sedgwick,‡ at the time when the dorsal portions of the mesoblastic somites have attained their maximum development. Bearing in mind that the dorsal sac of *Palæmonetes* has been formed by the

* Milne Edwards, 'Histoire naturelle des Crustacés,' Paris, 1834.

† Claus, C., "Zur Kenntniss der Kreislauforgane der Schizopoden und Decapoden." 'Arb. Zool. Inst. Wien,' vol. 5, 1884.

‡ Sedgwick, A., "The Development of the Cape Species of *Peripatus*." Parts I—IV. 'Quart. Journ. Micr. Sci.,' vols. 25—28, 1885—88.

union of two lateral cavities, which lay on either side of the aorta, the differences between the two forms are very slight. The dorsal sac represents the two dorsal portions of the mesoblastic somites, whilst the central cavity, the lateral cavities, and the nephridia agree, with the one exception that the two lateral portions of the nerve cord of *Peripatus* have united in the middle line in *Palæmonetes*, and in the process have passed out of the lateral cavities. The agreement is so close that it appears to me to be fully justifiable to homologise the various parts. If this be so, it follows that the dorsal sac of *Palæmonetes* is homologous with the dorsal portions of the mesoblastic somites of *Peripatus*, and that its cavity is a true cœlom. The central and lateral cavities, together with the cavities of the legs, will represent the pseudocœle, and being filled with blood may be termed, with Lankester, *hæmocœle*.

Passing now to the posterior part of the thorax, the region of the heart, we find that the different cavities correspond with those which persist in the adult *Peripatus*. Heart, pericardium, and pericardial septum of *Palæmonetes* present exactly the same relations as in *Peripatus*, and are clearly homologous structures in the two animals. The central and lateral cavities only differ on account of the relative position of the nervous system, and this difference has already been accounted for. It must be noted, however, that in this region no nephridia are found in the cavities of the limbs. Beneath the anterior end of the pericardial septum are found, as has been already stated, the genital organs, and here also the comparison with *Peripatus* may be instituted. We find a similar agreement to that which existed in the other regions compared, and we may, with a considerable degree of probability, again homologise corresponding parts. The genital organs of *Palæmonetes* must then be regarded as the representatives, in this region, of the cœlom.

If the homologies here suggested are valid, the body cavity relations of the Crustaceans under consideration may be stated briefly thus: both enterocœle (true cœlom) and pseudocœle are present, the enterocœle consisting of the dorsal sac, the green gland, and shell gland, or the end sacs of these organs, together with the genital organs and their ducts, whilst the pericardial septum may be regarded as equivalent to portions of the walls of another part of the same structure.

The pseudocœle consists of the heart and arteries, the pericardial cavity, the central cavity of the thorax, with the lateral cavities and the cavities of the limbs, and the various sinuses of the abdomen. The pseudocœle is filled with blood, and hence can be termed a *hæmocœle*.

I hope, shortly, to publish a more detailed account, with figures, of the relations described in this communication.